LEAVING PATCHES: EFFECTS OF ECONOMY, DEPRIVATION, AND SESSION DURATION

DOUGLAS ELLIFFE, B. MAX JONES, AND MICHAEL DAVISON

THE UNIVERSITY OF AUCKLAND, NEW ZEALAND

Three pigeons pecked keys for food reinforcers in a laboratory analogue of foraging in patches. Half the patches contained food (were prey patches). In prey patches, pecks to one key occasionally produced a reinforcer, followed by a fixed travel time and then the start of a new patch. Pecks to another key were exit responses, and immediately produced travel time and then a new patch. Travel time was varied from 0.25 to 16 s at each of three session durations: 1, 4, and 23.5 hr. This part of the experiment arranged a closed economy, in that the only source of food was reinforcers obtained in prey patches. In another part, food deprivation was manipulated by varying postsession feeding so as to maintain the subjects' body weights at percentages ranging from 85% to 95% of their ad lib weights, in 1-hr sessions with a travel time of 12 s. This was an open economy. Patch residence time, defined as the time between the start of a patch and an exit response, increased with increasing travel time, and consistently exceeded times predicted by an optimal foraging model, supporting previously published results. However, residence times also increased with increasing session duration and, in longer sessions, consistently exceeded previously reported residence times in comparable open-economy conditions. Residence times were not systematically affected by deprivation levels. In sum, the results show that the long residence times obtained in long closed-economy sessions should probably be attributed to session duration rather than to economy or deprivation. This conclusion is hard to reconcile with previous interpretations of longer-than-optimal residence times but is consistent with, in economic terms, a predicted shift in consumption towards a preferred commodity when income is increased.

Key words: patch residence time, travel time, closed economy, session duration, food deprivation, key peck, pigeons

---

In the some-patches-are-empty foraging paradigm (e.g., McNamara & Houston, 1985), an animal forages for prey in a series of patches (Cowie, 1977), each of which may or may not contain a single prey item. If a patch does contain prey, the search time required to find that prey is variable. The animal may leave a patch at any point, but traveling to the next patch takes a certain amount of time. The main dependent variable is the time from patch entry until the animal leaves the patch. This is called patch residence time (Kamil, Misthal, & Stephens, 1993) or moving-on time (Brunner, Kacelnik, & Gibbon, 1992).

McNamara and Houston (1985) showed that γ_t, the rate of obtaining prey in this paradigm, depends jointly on p, the probability that each patch contains prey; λ, the probability of discovering prey, per second, in a patch that does contain prey; τ, the time required to travel between patches; and t, the patch residence time; according to

$$\gamma_t = \frac{p(1 - e^{-\lambda t})}{\tau + (1 - p)t + \frac{p}{\lambda}(1 - e^{-\lambda t})}. \quad (1)$$

Following Charnov's (1976) well-known marginal value theorem, McNamara and Houston predicted that an optimally foraging animal should adopt a residence time t that maximizes γ_t in Equation 1. This predicts that t will increase with increasing τ, decrease with increasing λ, and increase with increasing p.

Several researchers have investigated behavioral laboratory analogues of the some-patches-are-empty paradigm. Generically, these procedures comprise a series of trials on which two keys are lit. On one key, called the patch key, responses are reinforced according to a variable-interval (VI) schedule defined by λ, on a randomly chosen proportion p of the trials. Trials end after a reinforcer is delivered, or after a predefined maximum search time (usually 120 s), or after a

single response to the other key, called the exit key. Trial termination is followed by an experimenter-imposed travel time τ, either in blackout or with a fixed-interval or fixed-ratio response requirement. Any or all of τ, λ, and *p* may be manipulated between conditions.

Experiments using these procedures have supported McNamara and Houston's (1985) predictions at the ordinal level. For example, Kamil et al. (1993) found that residence time increased with increasing travel time with blue jays (*Cyanocitta cristata*) foraging for *Tenebrio* larvae. Both Davison and McCarthy (1994) and McCarthy, Voss, and Davison (1994) confirmed this result with pigeons responding for wheat reinforcers. Davison and McCarthy also confirmed the predicted ordinal effects of varying *p* and λ, and McCarthy et al. showed that residence time was unaffected by response requirements during the travel time. However, in all these cases, residence times were consistently and substantially longer than those predicted by Equation 1. The quantitative predictions of McNamara and Houston's model are therefore unsupported.

The growing interest in laboratory analogues of foraging in part represents an increased concern on the part of behavioral researchers with ecological validity, or the generalizability of laboratory results to behavior in the natural environment. In a related vein, a body of research investigating the economic context of behavioral experiments has developed (e.g., Hursh, 1980, 1984; Hursh & Bauman, 1987; Rachlin, Green, Kagel, & Battalio, 1976). In these terms, an experiment in which the subject's behavior entirely determines the total consumption of the reinforcer is said to be conducted within a closed economy. By contrast, an open economy is a procedure in which there is at least some measure of independence between consumption of the reinforcer and behavior. Hursh (e.g., 1980, 1984) has argued that most behavioral experiments employ completely open economies, because the subjects are maintained at a constant deprivation level by postsession feeding, yet economies in the natural environment tend to be more closed than open. For example, a foraging animal's consumption of food is presumably a function of those responses it emits that result in food availability.

The distinction between open and closed economies is of more than passing interest, because it turns out that the nature of the economy for the reinforcer partly determines many behavioral results. For example, in a closed economy, response rate increases with increasing fixed-ratio requirement (Collier, Hirsch, & Hamlin, 1972) to a point far beyond that which typically produces ratio strain in open economies (e.g., Felton & Lyon, 1966). Similarly, response rate on VI schedules increases with increasing reinforcer rate in open economies (e.g., Catania & Reynolds, 1968), but decreases in closed economies. This latter result applies to behavior on a single VI schedule (Hursh, 1978, 1984; Lucas, 1981) or on one concurrent VI alternative (Hursh & Natelson, 1981), and to the aggregate behavior on two concurrent (Hursh, 1978) or multiple (Elliffe & Davison, 1996) VI alternatives. Finally, choice between identical reinforcers in concurrent alternatives is unaffected by the nature of the economy, whether in a simple concurrent (Baum, 1972; Graft, Lea, & Whitworth, 1977; Hursh, 1978) or concurrent-chains (LaFiette & Fantino, 1989) schedule, but choice between successive alternatives in multiple schedules is strikingly different in open and closed economies (Elliffe & Davison, 1985, 1996; LaFiette & Fantino, 1988).

Given the interest in ecological validity shared by the foraging and economic approaches, it is surprising that foraging experiments have not been routinely conducted in closed economies. The economic context of reinforcement seems peculiarly relevant to experiments that explicitly attempt to model naturally occurring behavioral situations. Moreover, there are specific reasons to expect behavior in foraging procedures, like the some-patches-are-empty paradigm, to be influenced by economy. Hursh (1980, 1984) and Hursh and Bauman (1987) have shown that most of the effects of economy described above are consistent with an analysis in terms of elasticity of demand. In an open economy, demand is elastic, meaning that consumption of the reinforcer is highly sensitive to changes in its price or availability. In a closed economy, demand is inelastic, meaning that a constant level of consumption is defended against changes in price or availability, often requiring large increases in responding. If

the contingencies that determine residence time involve maximization of reinforcement, as the ordinal support for McNamara and Houston's (1985) model suggests, elasticity of demand and the nature of the economy seem to be potentially influential factors.

These considerations motivated the present experiment, which employed a procedure similar to that of Davison and McCarthy (1994) and McCarthy et al. (1994), but within a closed economy, in that pigeons earned their entire daily ration of food as reinforcers during the experiment. Because the most common way to arrange a closed economy also results in long experimental sessions and in low food-deprivation levels (i.e., body weights close to ad lib levels), we also manipulated session duration and food deprivation directly to assess the contribution those variables might have made to any difference between open- and closed-economy foraging behavior.

METHOD

Subjects

Three naive adult homing pigeons, numbered 250, 251, and 253, served as subjects. A 4th pigeon, numbered 252, died during the experiment. It was not replaced, and its data are not reported. Water and grit were freely available in each bird's experimental cage.

Apparatus

Each bird lived in a cage 375 mm high, 375 mm wide, and 380 mm deep. The back, left, and right walls of the cage were made of sheet metal, and the top, floor, and front wall consisted of metal bars. Each cage contained two wooden perches about 25 mm by 25 mm in cross-section, one mounted 75 mm from and parallel to the floor and front wall, and one mounted 75 mm from and parallel to the floor and right wall.

The right wall contained two translucent response keys, 25 mm in diameter (20 mm for Bird 251) and centered 197 mm apart (228 mm for Bird 251) and 223 mm above the perches. The left and right keys could be transilluminated green and yellow, respectively, and, when lit, could be operated by pecks of force exceeding 0.1 N. A wheat hopper was located behind an aperture (45 mm by 45 mm) centered 148 mm (128 mm for Bird 251) below the keys. During reinforcer delivery, this hopper was raised and illuminated for 3 s and the keylights were extinguished.

The cages were located in a room containing the home and experimental cages of about 100 other pigeons. A good deal of activity took place in this room throughout the day. The room's ambient lighting was on between 6:00 a.m. and 7:00 p.m. each day. All experimental events were controlled, and the data recorded, by an IBM-PC compatible computer running MED-PC® software.

Procedure

Following magazine training, autoshaping of the key-peck response, and reinforcement of responses to both keys on a variety of VI schedules, the main experimental procedure was instituted. The procedure consisted of a series of trials, called patches. The start of a patch was signaled by the illumination of the green left and yellow right keys. A randomly determined half (i.e., p in Equation 1 = .5) of the patches were prey patches (i.e., arranged food reinforcement). In a prey patch, pecks to the green left key (search responses) were reinforced according to a constant-probability VI 5-s schedule (i.e., λ in Equation 1 = .2). A single peck to the yellow right key (exit response) extinguished both keys and initiated a fixed-duration travel time during which responses had no consequences (Table 1). The same travel time also followed reinforcer delivery. The next patch began after the travel time.

The sequence of experimental conditions is shown in Table 1. In Conditions 1 and 2, a maximum patch duration of 120 s was arranged. That is, patches ended and travel time began after 120 s in a patch without either a reinforcer or an exit response. Conditions 3 and 4 arranged identical conditions except that there was no maximum patch duration. Because there was no apparent difference between the results of Conditions 1 and 3 or between Conditions 2 and 4, the practice of predetermining maximum patch duration was discontinued, and patches continued until either a reinforcer was delivered or an exit response was emitted throughout the rest of the experiment.

In different parts of the experiment, sessions ended after either 1, 4, or 23.5 hr. Six conditions arranging different travel times

Table 1

Sequence of experimental conditions, showing the part of the experiment to which each condition contributed, travel time (in seconds), session duration (in hours), open or closed economy, and, if any, arranged percentage of ad lib body weight. Condition 10, shown in parentheses, was not used in any analyses.

Condi-tion	Part	Travel time	Session dura-tion	Economy	Arranged % of ad lib weight
1	0	2	4	closed	none
2	0	12	4	closed	none
3	1	2	4	closed	none
4	1	12	4	closed	none
5	1	4	4	closed	none
6	1	0.25	4	closed	none
7	1	8	4	closed	none
8	1	16	4	closed	none
9	2	2	1	closed	none
(10	2	12	1	open	none)
11	2	4	1	closed	none
12	2	0.25	1	closed	none
13	2	8	1	closed	none
14	2	16	1	closed	none
15	3	12	1	open	85%
16	3	12	1	open	91%
17	3	12	1	open	89%
18	3	12	1	open	87%
19	3	12	1	open	93%
20	3	12	1	open	95%
21	4	2	23.5	closed	none
22	4	12	23.5	closed	none
23	4	4	23.5	closed	none
24	4	0.25	23.5	closed	none
25	4	8	23.5	closed	none
26	4	16	23.5	closed	none

(0.25, 2, 4, 8, 12, and 16 s, in an irregular order) were arranged at each session duration in Parts 1, 2, and 4. During these parts, the only food available to the birds was as reinforcement for responding on the search key (i.e., the economy was closed), except for Condition 10, in which postsession feeding was necessary for all birds to maintain body weights at acceptable levels. This may have been because Condition 10 was the first condition that arranged a long travel time, and therefore a lower reinforcer rate, in 1-hr sessions. Because Condition 10 was therefore conducted within an open economy, its data have been excluded from all analyses. In Part 3, travel time was always 12 s and session duration was always 1 hr. Six conditions were conducted at different deprivation levels, defined as percentages (85%, 87%, 89%, 91%, 93%, and 95%, in an irregular order) of ad lib body weight. These deprivation levels were

produced by manipulating the amount of postsession mixed grain, in multiples of 5 cc, given to the birds (i.e., the economy was open). The amount of grain was chosen so as to produce a body weight as close as possible to the target weight for that condition.

Each bird was removed from its cage to be weighed at about 7:30 a.m. each day. In Parts 1, 2, and 3, the experimental session began shortly afterwards. In Part 4, sessions began at midnight. Sessions were conducted 7 days each week, and each condition ran for 30 days (the same condition duration adopted by Davison & McCarthy, 1994).

The data recorded were the times at which patches started and those at which search responses, reinforcers, and exit responses occurred. The main dependent variable was patch residence time, defined as the time from the start of a patch until an exit response. Patches that ended in reinforcement were not included in this measure, but prey patches in which an exit response occurred before reinforcement were included.

RESULTS

The data (median percentage of ad lib body weight, total numbers of prey trials, no-prey trials, exit responses and reinforcers, and median residence time) from the last 10 sessions of each condition for each bird are shown in the Appendix. Note that, from Condition 3 onwards, the sum of the numbers of exit responses and reinforcers is up to 10 less than the total number of patches, because sessions often ended after a patch had begun but before either a reinforcer or an exit response occurred, resulting in one fewer patch termination than patch start being recorded for that session. We have preferred the median to the mean as an average for residence times because the frequency distributions of residence times are positively skewed. In particular, because no maximum patch duration was arranged from Condition 3 onwards, there were some residence times of several hours in Part 4 (23.5-hr sessions), presumably while the subjects were sleeping.

Figure 1 shows median residence time as a function of travel time for each bird and the mean of all birds at session durations of 1, 4, and 23.5 hr (Parts 2, 1, and 4, respectively). The optimal residence times derived from
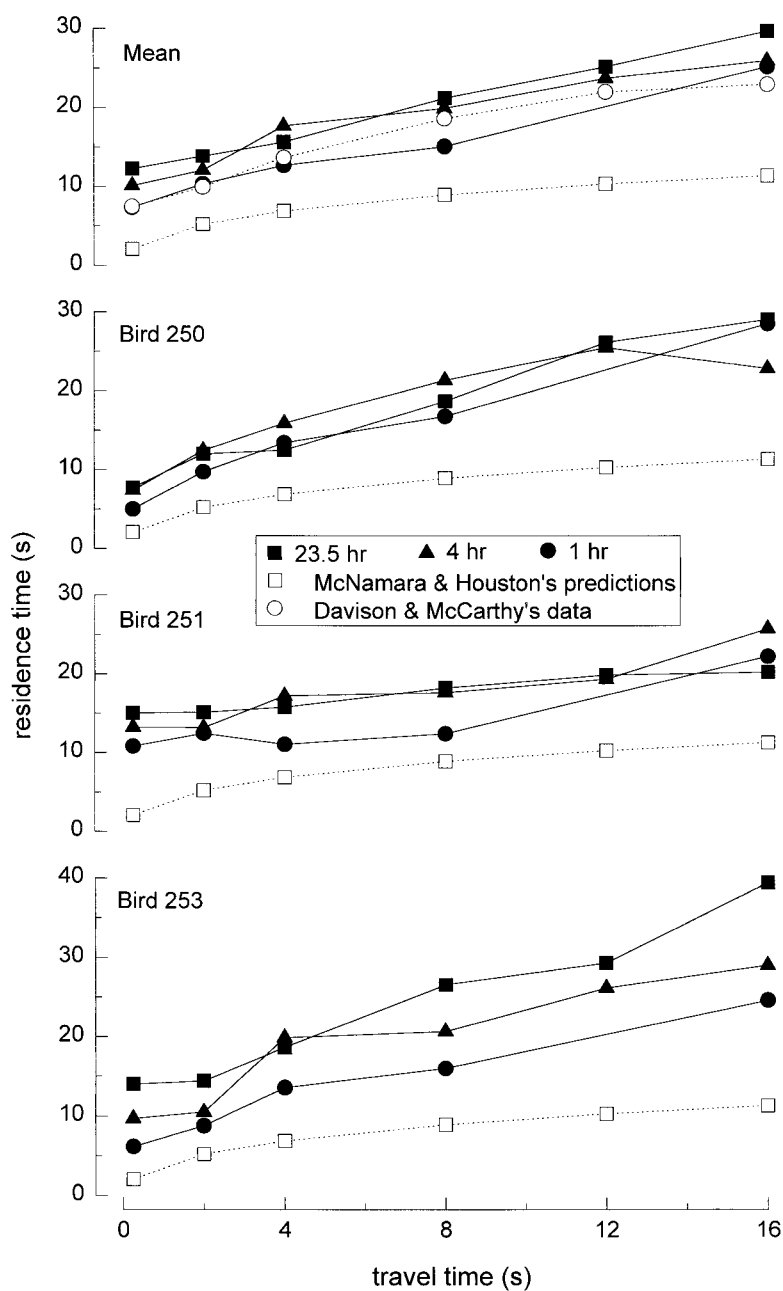
Fig. 1.   Median residence time (in seconds) as a function of travel time (in seconds) for each bird and the mean of all birds in 1-hr (filled circles), 4-hr (filled triangles), and 23.5-hr (filled squares) sessions. The optimal residence times (open squares) predicted from McNamara and Houston's (1985) equation and, on the mean plot, the mean residence times (open circles) obtained under comparable conditions in 45-min open-economy sessions by Davison and McCarthy (1994) are also shown.

Equation 1 are shown for comparison, as are the mean residence times, across subjects, obtained by Davison and McCarthy (1994) in 45-min open-economy sessions at the same values of τ, λ, and p.

An exact-probability version[1] of Kendall's (1955) nonparametric, rank-randomization trend test showed that median residence time increased systematically both with increasing travel time ($\Sigma S = 112$, $z > 9.00$, $p < .001$) and, although generally by small amounts, with increasing session duration ($\Sigma S = 30$, $z = 3.90$, $p < .001$). At all session durations, every median residence time was longer than the optimal prediction for that travel time ($N = 51$, binomial $p < .001$). Residence times from 1-hr sessions did not differ reliably from those obtained by Davison and McCarthy (1994) under similar, but open-economy, conditions (binomial $p > .05$). However, residence times from 4-hr and 23.5-hr sessions were always longer than those obtained by Davison and McCarthy under comparable conditions (binomial $p < .001$).

Although reliable, the relationship between residence time and session duration is not immediately apparent in Figure 1. Figure 2 presents the same data again, but arranged by session duration in bar graphs for each bird at each travel time. The small but systematic increase in residence time with increasing session duration is readily seen as an upward trend in residence time bars moving from left to right within each travel time.

In the closed-economy conditions (Parts 1, 2, and 4), body weight increased systematically with increasing session duration across birds and travel times (nonparametric trend test: $\Sigma S = 23$, $z = 3.10$, $p < .001$). The mean percentages of ad lib body weight, across birds, maintained in 1-hr, 4-hr, and 23.5-hr sessions were 89%, 93%, and 96%, respectively. Davison and McCarthy (1994) maintained their pigeons at 85% of ad lib weight. To assess a possible direct relationship between deprivation and residence times, Part 3 ma-

nipulated body weight directly within a similar range (85% to 95% ad lib weight in 2% steps) by varying the amount of postsession food. This manipulation produced median body weights, over the last 10 days of each condition, very close to those intended. Most (15 of 18) median body weights were within 0.5% (about 2.5 g) of their target weights, and only one median body weight differed from its target weight by more than 1% (Bird 251 in Condition 15 was 1.02% below its target). Figure 3 shows median residence times as a function of obtained percentage of ad lib body weight for each bird in each condition of Part 3. There was no consistent trend across birds in residence time with changes in body weight (nonparametric trend test: $\Sigma S = 11$, $z = 1.08$, $p > .05$).

DISCUSSION

The purpose of this experiment was to compare the effect of arranging the some-patches-are-empty foraging paradigm in a closed economy with the well-established results obtained in open economies (e.g., Davison & McCarthy, 1994; Kamil et al., 1993). As in open economies, residence time increased with increasing travel time and was longer than optimal. This reconfirms the ordinal, but not quantitative, predictions of McNamara and Houston's (1985) equation. Both Brunner et al. (1992) and Davison and McCarthy have advanced reasons why residence times might be systematically longer than optimal. In essence, their interpretations rest on the fact that the decrease from the maximum reinforcer rate sustained by deviations from optimal towards longer residence times is less than the decrease sustained by equal-sized deviations towards shorter residence times. Thus, if there is any variance or error in residence times, a bias towards staying longer than optimal in a patch is to be expected.

However, residence times obtained under both 4-hr and 23.5-hr closed-economy conditions in Parts 1 and 4 of this experiment were reliably further from optimal than those obtained by Davison and McCarthy (1994) in equivalent open-economy conditions. Given the presumably greater importance to survival of maximizing food consumption (decreased elasticity of demand for food) in a

---

[1] Because there were unequal numbers of travel times at the different session durations, Kendall's (1955) tables and normal approximation could not be used. The exact probabilities of the obtained values of Kendall's test statistic ΣS were therefore calculated by randomization of ranks. The quoted values of z refer to the best fitting normal approximation to the exact sampling distribution of ΣS in each case.
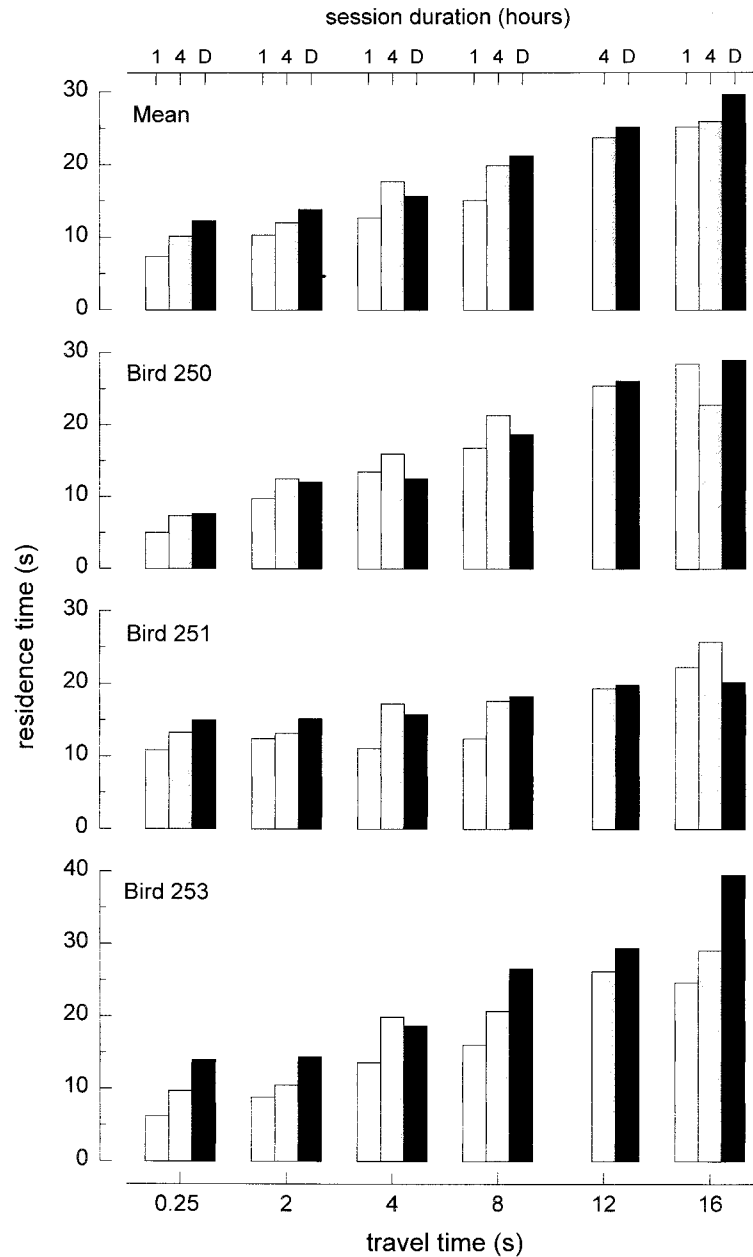
Fig. 2.   Median residence time (in seconds) at each session duration and travel time for each bird and the mean of all birds in Parts 1, 2, and 4. Within the row of bar graphs for each bird, travel time increases from left to right (lower *x* axis). Within each bar graph, session duration increases from 1 hr (white bars) through 4 hr (gray bars) to 23.5 hr (black bars, labeled D on axis), from left to right (upper *x* axis).

closed economy, this result surprised us. From Davison and McCarthy's and Brunner et al.'s (1992) interpretations, or indeed any other optimality account, we had expected a move towards optimal residence times.

Because part of the following discussion rests on a between-experiments comparison of our data with those of Davison and Mc-Carthy (1994), it is worth considering poten-tially influential procedural differences be-tween the two studies. Both arranged the same probability of prey trials (p), rate of prey
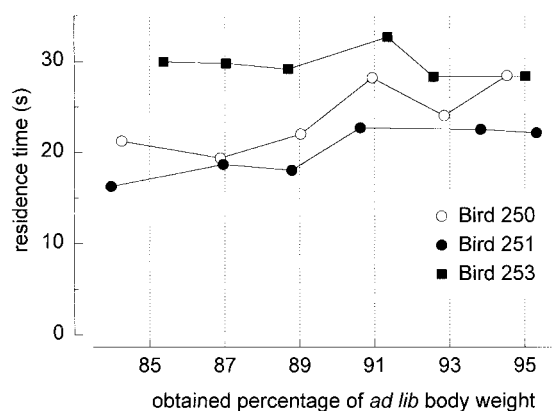
Fig. 3.   Median residence time (in seconds) as a function of food deprivation level, expressed as a percentage of ad lib weight, for each bird in each condition of Part 3.

arrival (λ), and set of travel times. Neither arranged a trial-start response (cf. Kamil et al., 1993). The species was the same, as was the laboratory and most aspects of the apparatus. The apparatus differed in three, almost certainly minor, respects. The keys were red and white, rather than yellow and green, in Davison and McCarthy's experiment, and were slightly closer together (130 mm apart). Davison and McCarthy placed their birds in the experimental chamber for the duration of the session only, rather than attaching the experimental apparatus to each bird's home cage, as we did. None of these differences seems likely to have had a systematic effect on residence times, and we argue that a direct comparison between our closed-economy data in 1-hr sessions and their open-economy data in 45-min sessions is justified.

Apart from the nature of the economy, there were two potentially important differences between the 23.5-hr closed-economy conditions of Part 4 and Davison and McCarthy's (1994) open-economy experiment. First, the experimental sessions were much longer. Second, the amount of food reinforcement delivered each day was sufficient to maintain the birds at about 96% of their ad lib body weights, in contrast with the usual practice of maintaining subjects at about 85% of ad lib weight in open-economy experiments. Direct effects of both session duration and the level of food deprivation on other aspects of behavior have often been reported (e.g., Charman & Davison, 1983; Elliffe & Davison, 1996; Herrnstein & Loveland, 1974). Parts 1, 2, and

3 of this experiment were therefore included to assess the extent to which differences in session duration and deprivation level contributed to the difference between residence times in Part 4 and typical open-economy residence times. The range of deprivation levels arranged (85% to 95% of ad lib weight) equates to the difference in deprivation between our 23.5-hr conditions and Davison and McCarthy's study. As Figure 3 shows, the deprivation levels actually maintained in Part 3 were close to those arranged.

The results of Part 3 (Figure 3) showed that residence times were not consistently affected by deprivation level, at least with these experimental parameters. Although the curves for 2 of the birds appear to show a small trend toward increasing residence times with higher body weight, the trend for the other bird was opposite in direction, and there was no overall significant trend. On the basis of these data, there is no reason to attribute the long residence times obtained in Part 4 to high body weights or low deprivation levels.

By contrast, Figures 1 and 2 show that residence time increased systematically with increasing session duration across Parts 2, 1, and 4. Indeed, residence times in 1-hr closed-economy sessions in Part 2 did not differ reliably from those obtained by Davison and McCarthy (1994) in 45-min open-economy sessions. This suggests that, on the grounds of parsimony, the difference between residence times in both 4-hr and 23.5-hr closed-economy sessions (Parts 1 and 4) and Davison and McCarthy's results should probably be attributed to the increased session duration rather than to the change in economy.

This conclusion does not seem to be easily interpretable in terms of deviations from optimality. We can see no reason to predict that session duration should, independent of economy or deprivation, directly affect any tendency to behave optimally. One interpretation does suggest itself to us, but it owes more to behavioral economics than to optimal foraging theory. Hursh and Bauman (1987) proposed that animals might stay in a patch longer than optimal because the more immediate prey in the current patch is a commodity that is preferred to the temporally distant prey in future patches. That is, prey items in the current and future patches do

not interact as perfectly substitutable commodities, as is implicitly assumed by McNamara and Houston's (1985) equation. If this interpretation is correct, mechanisms that rely on maximizing overall reinforcer rate can never fully describe foraging behavior, because the individual reinforcers making up that overall rate are not perfect substitutes. (Hursh, e.g., 1980, made a similar argument with respect to the conditions that limit strict matching in concurrent schedules.)

In our experiment, changing session duration may be seen in economic terms as an income manipulation (e.g., Hursh, 1984). In microeconomics, the general predicted effect of increasing income is to shift consumption towards preferred commodities. If it is true that prey in the current patch is a preferred commodity, increasing session duration, and therefore income, should increase the tendency to search longer for that preferred commodity in the current patch. This predicts an increasing deviation from optimal and towards longer residence times, as we found.

In conclusion, we found that residence times increased with travel times, but were longer than optimal, in closed economies. This is consistent with the growing literature on foraging in this paradigm in open economies. However, residence times in long closed-economy sessions were even further from optimal than they were in published open-economy studies under comparable conditions. The results of arranging short closed-economy sessions and manipulations of both session duration and deprivation level suggest that this effect should probably be attributed to session duration rather than to the type of economy. This conclusion is difficult to interpret in a manner consistent with previous explanations of deviations from optimality. Tentatively, we offer a possible interpretation derived from behavioral economics.

REFERENCES

Baum, W. M. (1972). Choice in a continuous procedure. *Psychonomic Science, 28,* 263–265.

Brunner, D., Kacelnik, A., & Gibbon, J. (1992). Optimal foraging and timing processes in the starling, *Sturnus vulgaris*: Effect of inter-capture interval. *Animal Behaviour, 44,* 597–613.

Catania, A. C., & Reynolds, G. S. (1968). A quantitative analysis of the responding maintained by interval schedules of reinforcement. *Journal of the Experimental Analysis of Behavior, 11,* 327–383.

Charman, L., & Davison, M. (1983). On the effects of food deprivation and component reinforcer rates on multiple-schedule performance. *Journal of the Experimental Analysis of Behavior, 40,* 239–251.

Charnov, E. L. (1976). Optimal foraging: The marginal value theorem. *Theoretical Population Biology, 9,* 129–136.

Collier, G., Hirsch, E., & Hamlin, P. H. (1972). The ecological determinants of reinforcement in the rat. *Physiology and Behavior, 9,* 705–716.

Cowie, R. J. (1977). Optimal foraging in great tits (*Parus major*). *Nature, 268,* 137–139.

Davison, M., & McCarthy, D. (1994). Leaving patches: An investigation of a laboratory analogue. *Journal of the Experimental Analysis of Behavior, 62,* 89–108.

Elliffe, D., & Davison, M. (1985). Performance on continuously available multiple schedules. *Journal of the Experimental Analysis of Behavior, 44,* 343–353.

Elliffe, D., & Davison, M. (1996). Continuous multiple-schedule performance: Effects of deprivation and session duration. *Journal of the Experimental Analysis of Behavior, 65,* 111–128.

Felton, M., & Lyon, D. O. (1966). The post-reinforcement pause. *Journal of the Experimental Analysis of Behavior, 9,* 131–134.

Graft, D. A., Lea, S. E. G., & Whitworth, T. L. (1977). The matching law in and within groups of rats. *Journal of the Experimental Analysis of Behavior, 27,* 183–194.

Herrnstein, R. J., & Loveland, D. H. (1974). Hunger and contrast in multiple schedules. *Journal of the Experimental Analysis of Behavior, 21,* 511–517.

Hursh, S. R. (1978). The economics of daily consumption controlling food- and water-reinforced responding. *Journal of the Experimental Analysis of Behavior, 29,* 475–491.

Hursh, S. R. (1980). Economic concepts for the analysis of behavior. *Journal of the Experimental Analysis of Behavior, 34,* 219–238.

Hursh, S. R. (1984). Behavioral economics. *Journal of the Experimental Analysis of Behavior, 42,* 435–452.

Hursh, S. R., & Bauman, R. (1987). The behavioral analysis of demand. In L. Green & J.H. Kagel (Eds.), *Advances in behavioral economics* (Vol. 1, pp. 117–165). Norwood, NJ: Ablex.

Hursh, S. R., & Natelson, B. H. (1981). Electrical brain stimulation and food reinforcement dissociated by demand elasticity. *Physiology and Behavior, 26,* 509–515.

Kamil, A. C., Misthal, R. L., & Stephens, D. W. (1993). Failure of simple optimal foraging models to predict residence time when patch quality is uncertain. *Behavioral Ecology, 4,* 350–363.

Kendall, M. G. (1955). *Rank correlation methods*. London: Charles Griffin.

LaFiette, M. H., & Fantino, E. (1988). The effects of component duration on multiple-schedule performance in open and closed economies. *Journal of the Experimental Analysis of Behavior, 50,* 457–468.

LaFiette, M. H., & Fantino, E. (1989). Responding on concurrent-chains schedules in open and closed economies. *Journal of the Experimental Analysis of Behavior, 51,* 329–342.

Lucas, G. A. (1981). Some effects of reinforcer availability on the pigeon's responding in 24-hour schedules. *Animal Learning & Behavior, 9,* 411–424.

McCarthy, D., Voss, P., & Davison, M. (1994). Leaving patches: Effects of travel requirements. *Journal of the Experimental Analysis of Behavior, 62,* 185–200.

McNamara, J., & Houston, A. (1985). A simple model of information use in the exploitation of patchily distributed food. *Animal Behaviour, 33,* 553–560.

Rachlin, H., Green, L., Kagel, J. H., & Battalio, R. C. (1976). Economic demand theory and psychological studies of choice. In G. H. Bower (Ed.), *The psychology of learning and motivation* (Vol. 10, pp. 129–154). New York: Academic Press.

APPENDIX

Data for each subject summed over the last 10 days of each condition. The residence times are medians, and percentages of ad lib weight are medians.

Condition	% ad lib weight	Prey trials	No-prey trials	Exits	Reinforcers	Residence time (s)
Bird 250						
1	94	1,947	1,861	1,569	1,537	16.05
2	92	1,655	1,711	1,470	1,586	28.69
3	93	1,768	1,744	1,981	1,523	12.47
4	93	1,437	1,452	1,496	1,383	25.46
5	89	1,130	1,173	1,276	1,019	15.93
6	88	2,528	2,533	3,406	1,645	7.39
7	91	1,922	1,924	2,005	1,832	21.35
8	91	1,785	1,828	1,887	1,719	22.79
9	90	1,328	1,352	1,646	1,026	9.75
11	87	1,121	1,171	1,294	989	13.44
12	92	1,929	1,984	2,760	1,143	5.02
13	88	842	834	879	793	16.78
14	87	438	455	461	428	28.48
15	84	606	584	590	595	21.26
16	91	309	354	354	299	28.19
17	89	614	610	625	594	22.02
18	87	707	645	674	671	19.41
19	93	317	299	308	298	24.01
20	95	274	229	235	259	28.38
21	93	2,459	2,569	2,914	2,104	12.03
22	91	2,053	2,034	2,082	1,995	26.12
23	97	2,125	2,101	2,394	1,822	12.49
24	102	2,292	2,307	3,011	1,578	7.73
25	104	1,696	1,677	1,763	1,600	18.69
26	101	1,726	1,763	1,787	1,692	29.00

APPENDIX

(Continued)

Condition	% ad lib weight	Prey trials	No-prey trials	Exits	Reinforcers	Residence time (s)
Bird 251						
1	100	2,350	2,346	2,228	1,738	12.84
2	97	1,832	1,903	1,752	1,632	22.45
3	99	2,033	2,033	2,322	1,734	13.21
4	91	1,994	2,084	2,190	1,880	19.38
5	97	1,912	1,881	2,028	1,755	17.26
6	97	2,332	2,359	2,954	1,727	13.25
7	97	2,073	3,095	2,196	1,963	17.66
8	87	1,537	1,554	1,572	1,512	25.81
9	92	1,452	1,413	1,607	1,250	12.47
11	87	1,135	1,140	1,289	982	11.08
12	93	1,512	1,582	1,855	1,229	10.85
13	90	982	978	1,072	883	12.46
14	88	251	285	280	246	22.30
15	84	574	644	673	538	16.31
16	91	225	238	237	216	22.69
17	89	475	531	543	455	18.07
18	87	617	697	717	594	18.71
19	94	287	309	308	278	22.49
20	95	181	193	188	177	22.11
21	93	1,857	1,868	2,121	1,594	15.17
22	93	1,276	1,296	1,358	1,204	19.91
23	93	1,215	1,289	1,406	1,088	15.79
24	92	1,346	1,294	1,488	1,142	15.03
25	90	1,164	1,105	1,182	1,077	18.27
26	88	1,043	972	1,001	1,004	20.26
Bird 253						
1	98	2,247	2,210	2,058	1,616	10.51
2	95	1,961	1,928	1,751	1,814	19.64
3	97	2,155	2,231	2,579	1,797	10.52
4	94	1,049	1,102	1,142	999	26.21
5	88	676	626	672	620	19.91
6	91	2,029	1,955	2,575	1,399	9.71
7	94	1,976	1,893	1,988	1,872	20.72
8	89	1,683	1,724	1,737	1,663	29.11
9	88	1,618	1,647	2,010	1,249	8.83
11	89	1,080	1,032	1,160	943	13.59
12	95	2,751	2,663	3,843	1,563	6.20
13	90	819	864	909	767	16.04
14	87	507	508	517	492	24.67
15	85	482	488	491	471	29.96
16	91	530	484	487	519	32.65
17	89	535	522	527	522	29.16
18	87	510	483	489	498	29.79
19	93	591	563	569	578	28.27
20	95	535	502	501	530	28.31
21	101	2,135	2,079	2,379	1,825	14.41
22	100	1,099	1,037	1,065	1,061	29.40
23	100	1,820	1,824	1,978	1,656	18.69
24	101	1,104	1,148	1,367	875	14.01
25	100	1,254	1,273	1,321	1,196	26.60
26	97	1,315	1,356	1,370	1,291	39.55